ON SUCCESSIVE, PROTANDRIC AND PROTEROGYNIC HERMAPHRODITISM IN ANIMALS.

By Thos. H. Montgomery, Jr., Ph. D.

The term Successive Hermaphroditism has been introduced (Claparède, 9) to designate the kind of Hermaphroditism present in those animal forms, where the male and female gonads (germ glands) are in the adult separated from each other, and where the sexual products (sperma, ova) of the one sex develop earlier than those of the other. In all known cases of this form of Hermaphroditism, with perhaps the single exception of *Microstoma lineare* (Rywosch, 39, 40), the male products develop first.

Successive Hermaphroditism is prevalent in the *Plathelminthes* (with the exception of the Nemerteans) and especially in the group of the *Turbellaria*. In the *Cestodes* it has been observed in *Solenophorus megalocephalus* (Rodoz, 38) and by Zschokke (48) in *Cestodes* which present a large number of proglottids. Ercolani (15) has proved this phase of Hermaphroditism among certain *Distomids*. In the *Turbellaria* it occurs in probably all the *Acoela* (Graff, 16). Among *Rhabdocœlida* in *Convoluta* (Claparède, 9), in *Macrostoma hystrix* and *Promeostoma ovoideum* (Graff, 16), in *Graffilla muricicola* (Ihering, 18, Böhmig, 5) and in *G. brauni* (Smidt, 42), in *Prorhynchus* (von Kennel, 19, Moore, 32a). According to Du Plessis (13) it occurs in *Plagiostoma lemani*, though the accuracy of this observation has been doubted by Graff (*l. c.*). As mentioned above, in *Microstoma lineare* according to Rywosch (39, 40) the female organs develop before the male organs. Hallez (17) has observed this phase of Hermaphroditism in a number of the *Tricladidea*, and Loman (29) in *Bipalium*. It is the rule in the *Polycladidea* (Lang, 24). Finally, Successive Hermaphroditism has been noted among the *Mollusca* in *Entoconcha* (Müller, 33), and in the *Anatinacea* (Babor, 2).

In the case of Protandric Hermaphroditism the male and female gonads are united together into a single herma-

phrodite gland (ovotestis), but the male elements are developed earlier than the female. Protandric and Successive Hermaphroditism are, however, not to be very sharply distinguished from one another. For example, in the Molluscs, where both these phases occur, we find all intermediate stages between (1) forms having a simple ovotestis, in which the male elements develop first (e. g. *Ostrea*); (2) forms, where in certain acini of a protandric ovotestis only male, in other acini only female elements are produced (e. g. *Lobiger*); and lastly (3) in forms where there are two or four separate genital glands, the male elements developing first (e. g. *Entoconcha* and the *Anatinacea*). According, though it is not proved that in all cases Successive Hermaphroditism has been evolved out of Protandric Hermaphroditism, this has very probably been the case in certain animals, as *Entoconcha* and the *Anatinacea*, which shows that these two phases of Hermaphroditism are closely connected with each other.

Protandric Hermaphroditism has been demonstrated in representatives of a large number of groups. Among sponges in *Aplysilla violacea* (Lendenfeld, 26) and *Amorphina coalita* (Topsent, 44); I wish here to express my thanks to my former teacher, Prof. F. E. Schulze of Berlin, for calling my attention to these two references. Among *Nematodes* in *Allantonema mirabile* (Leuckart, 28), and *Filaria rigida* (zur Strassen, 43). Among *Nemertinea* in *Tetrastemma kefersteini* (Marion, 30), and observed further by me (32) in *Stichostemma eilhardi*. According to Korschelt's (21) observations it is present in the polychæte Genus *Ophryotrocha*. Wheeler's (46) account of the development of the gonads of *Myzostoma* would show that in this form Protandric Hermaphroditism exists, though Beard's (3, 4) studies on the contrary would explain the state of affairs on the "complemental male" theory. Among Isopod Crustacea in three genera of the *Cymothoidæ*,-*Nerocila*, *Cymothoa*, *Anilocra* (Mayer, 31). Among *Echinoderms* we find it in *Asterina gibbosa* and *Amphiura squamata* (Lang, 25). But especially in the *Mollusca* is Protandry of frequent occurrence. So it occurs in the *Solenogastra* (Wiren, 47, Koren, and Danielssen, 20). In the *pulmonate Gasteropoda* in *Lymnæus* (Eisig, 14),

Agriolimax agrestis L. and *A. melanocephalus* Kal. (Babor, 1, 2). In the *Opisthobranch Gasteropoda* in *Cymbulia* (Leuckart, 27), *Cymbuliopsis* (Peck, 35); *Desmopterus papilio* (Chun, 8); *Lobiger, Clio striata, Clione, Eolis* and *Elysia* (Pelseneer, 36, 37). Among the *Lamellibranchiata* in *Ostrea* (Davaine, 12, confirmed by Van Beneden, 45). Finally, among the Vertebrates in *Myxine* (Cunningham, 11, Nansen, 34), and in *Chrysophrys* (Brock, 6).

Proterogynic Hermaphroditism is the term applied to the case of those animals, where the male and female gonads are not morphologically separate from each other, and where in the single ovotestis the female genital products are developed before the male products. It is much more restricted than the two other phases of Hermaphroditism under discussion, thus far having been observed only in pulmonate Gastropoda,—*Limax maximus* L., *Malacolimax tenellus* Nils. (Babor, 1, 2), *Agriolimax lævis* Müll. (Brock, 7; Babor, 1, 2); and among the *Tunicata* in *Salpa* (Krohn, 23; Korschelt and Heider, 22).

Since now both Proterogynic and Protandric Hermaphroditism may occur in the same genus (e. g. *Agriolimax*), these two phases of Hermaphroditism are probably closely allied. And as there exists in some cases of Protandry a cycle of development, where the individual is first male, then hermaphrodite, then female (e. g. *Stichostemma*); so there is present in some cases of Proterogyny (e. g. *Agriolimax lævis*) a similar ontogenetic cycle, only reversed, by which the individual is first female, then hermaphrodite, and lastly becomes male. In fact, I think that I am justified in concluding, that the three forms of Hermaphroditism, which form the subject of the present paper, are closely connected with each other, and their differences are more of degree than of kind.

What light does the consideration of these three phases of Hermaphroditism throw on the much discussed question,—whether in the Metazoa the hermaphroditic or whether the dioecious state should be regarded as the more primitive? Now we have found that in each phase, the products of the one sex develop earlier than the products of the other sex; accordingly, judging from the well known biogenetic law, that the

ontogeny repeats (to some extent at least) the phylogeny, we may logically conclude that the Hermaphroditism of those *Metazoa*, which present one or another of these phases of sexual development, has been secondarily acquired. This seems to me to be the only adequate explanation for such cycles of sexual development in the individual. Since the object of my present paper is only to discuss the meaning of these three kinds of Hermaphroditism, it would be irrelevant to bring into consideration the many other reasons tending to show that Hermaphroditism in the *Metazoa* is a secondarily acquired state. But this much may be remarked, that according to our argument all animal forms which present one or another of these phases of Hermaphroditism have been developed from dioecious ancestral forms; and it must be left to future investigators to show in how many forms these phases are actually present, that is, whether or not all hermaphrodite *Metazoa* are either protandric, proterogynic, or successively hermaphrodite, and whether or not all hermaphrodite *Metazoa* are, therefore, to be regarded by the argument above as having been derived from dioecious ancestors. Finally in those forms where the individual is first male (or female), then becomes hermaphroditic, and lastly female (or male), we may conclude that the hermaphrodite species in question has not only been evolved out of dioecious ancestral forms, but is perhaps also tending to become dioecious for a second time.

There now arises the question: on which sex has the hermaphroditic state been superimposed? In the case of protandric hermaphrodites, since here the male stage appears first in the ontogeny, one must suppose that it has been imposed on the male,—that ova have appeared in the testicle, and the individual has thus become hermaphroditic. Similarly, in all cases of Successive Hermaphroditism with perhaps the exception of *Microstoma lineare*, we may consider that here too the Hermaphroditism has been superimposed on male individuals. In proterogynic forms, on the contrary, the Hermaphroditism has probably been imposed on the female, since here the female stage appears ontogenetically first. Pelseneer (37) while arguing that all hermaphrodite molluscan forms have

been developed out of dioecious ancestors, endeavors to prove, that hermaphroditism here has been superimposed on the female sex alone. He bases his assumption on the fact, that in certain normally hermaphroditic Gastropods (*Cymbuliopsis, Clio striata, Helix aspera, Agriolimax lævis, Arion intermedius*) whenever an individual is found which is not hermaphroditic, it possesses the female organs only. But *Agriolimax lævis* is certainly, and *Helix* and *Arion* probably, proterogynic, so that the individuals found with female organs only, should simply be considered as individuals in the early stage before male organs have appeared. *Clio striata* on the contrary, and probably *Cymbuliopsis*, are protandric, accordingly the annotated female individuals of these two species should be regarded, as being individuals which have passed through both the early male and the hermaphroditic stage, and through the loss of all male elements had become entirely female. Thus Pelseneer's five cited cases are to be explained as being individuals in certain stages of ontogenetic sexual development, and are not to be referred to Atavism. To summarize, I agree with this zoologist that Hermaphroditism has been evolved out of the female state in all proterogynic forms, but in opposition to his views, hold that in the case of protandric forms Hermaphroditism has been superimposed on the male sex.

As to those forms, in which so-called "complemental males" are present (e. g. the *Cirripedea*, and, perhaps, *Myzostoma*), I think that these too may come under either the conception of Protandric or of Proterogynic Hermaphrodites. The complimental males could then, in the case of Protandry, be regarded as individuals which had not yet become hermaphroditic; and in the case of Proterogyny, as individuals which had passed through the ontogenetic female and hermaphroditic stages, and had become entirely male. It is perhaps more probable that Protandry and not Proterogyny has been the method of development in the Cirripedes. However, until our knowledge of ontogeny of the Cirripedes has advanced much further than its present state, the suggestions here advanced to account for the existence of complemental males can only be regarded in the light of a hypothesis.

List of Works Cited.

1. **Babor, J. & Kostal, J.,** Příspěvky ku poznání poměru pohlavních u některých Limacidů. Vestník Kral. Ceske. spol. nauk. v Praze., 1893.

2. **Babor, J. F.,** Ueber den Cyclus der Geschlechtsentwicklung der Stylommatophoren. Verhandl. deutsch. Zool. Gesell. 1894. (Leipzig.)

3. **Beard, J.,** On the Life-History and Development of the Genus Myzostoma (F. S. Leuckart), Mittheil. zool. Stat. Neapel. V, 1884.

4. **Beard, J.,** The Nature of the Hermaphroditism of Myzostoma. Zool. Anz. 461, 1894.

5. **Böhmig, L.,** Untersuchungen über rhabdocöle Turbellarien. Das Genus Graffilla v. Ihering. Zeitschr. f. wiss. Zool. 43, 1886, p. 290.

6. **Brock, J.,** Beiträge zur Anatomie und Histologie der Geschlechtsorgane der Knochenfische. Morphol. Jahrb. IV, 1878. (S. 569.)

7. **Brock, J.,** Die Entwicklung des Geschlechtsapparates der stylommatophoren Pulmonaten, etc. Zeitschr. f. wiss. Zool. 44, 1886.

8. **Chun, C.,** Bericht über eine nach den Canarischen Inseln im Winter, 1877–'8 ausgeführte Reise. Sitzungsb. k. preuss. Akad. d. Wissensch. Berlin, 1889.

9. **Claparède, Ed.,** Recherches anatomiques sur les Annélides Turbellariés, Opalines et Gregarines Observés dans les Hébrides. Mém. Soc. de Phys. et d'hist. nat. de Genève, XVI, 1861 (p. 128.)

10. **Collinge, W. E.,** On the Absence of the Male Reproductive Organs in two Hermaphrodite Molluscs. Journ. of Anat. & Physiol. 27, 1893 (p. 237.)

11. **Cunningham, J. T.,** On the Structure and Development of the Reproductive Elements in Myxine glutinosa, L. Quart. Journ. Micr. Sci. XXVII, 1887 (p. 49.)

12. **Davaine, C.,** Recherches sur la Génération des Huitres. Mém. Soc. de Biol. Paris, 1853.

13. **Du Plessis, G.**, Turbellariées limicoles. Bull. Soc. Vaud. Sc. Nat. XIII, 1874 (p. 114.)

14. **Eisig, Hugo**, Beiträge zur Anatomie und Entwicklungsgeschichte der Geschlechtsorgane von Lymnæus. Zeitschr. f. wiss. Zool. 19, 1869.

15. **Ercolani, G.**, Dell'adattamento della specie all'am biente. Nuove ricerche sulla storia genetica dei Trematodi. Memoria II. Mem. Acc. Sci. Ist. Bologna. 3, 1882 (p. 43.)

16. **Graff, L. v.**, Monographie der Turbellarien. I, Rhabdocoelida. Leipzig, 1882 (p. 127.)

17. **Hallez, P.**, Contributions a l'histoire naturelle des Turbellariés. Lille, 1879 (p. 43.)

18. **Ihering, H. v.**, Graffilla muricicola, eine parasitische Rhabdocöle. Zeitschr. f. wiss. Zool. XXIV, 1880 (p. 147.)

19. **Kennel, S. v.**, Zur Anatomie der Gattung Prorhynchus. Arbeit.-zool.-zoot. Instit. Würzburg, 6, 1882, (p. 69.)

20. **Koren, J. & Danielssen, D. C.**, Beskrivelse over nye Arter, henhörende til Slaegten Solenopus, samt nogle Oplysninger om dens Organisation. Archiv. f. Mathematik og Naturvidenskag. Christiania, 1877 (p. 120.)

21. **Korschelt, E.**, Ueber Ophryotrocha puerilis Clap.-Metsch. etc. Zeitschr. f. wiss. Zool. 57, 1894 (p. 272.)

22. **Korschelt, E. & Heider, K.**, Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere. III tes Heft. Jena, 1893 (p. 1333.)

23. **Krohn, M.**, Observations sur la génération et la développement des Biphores (Salpa). Ann. d. Sci. Nat. Paris, VI, 1846.

24. **Lang, A.**, Die Polycladen des Golfes von Neapel und der angrenzenden Meeresabschnitte. Fauna und Flora des Golfes von Neapel, XI, 1884 (p. 282.)

25. **Lang, A.**, Lehrbuch der vergleichenden Anatomie, IV. Abtheil. 1894 (p. 1091.)

26. **Lendenfeld, v.**, Ueber Cœlentraten der Südsee, II, Nene Aplysinidæ. Zeitschr. f. wiss. Zool. 38, 1883 (p. 261.)

27. **Leuckart, R.**, Zoologische Untersuchungen, III tes Heft. Giessen, 1854.

28. **Leuckart, R.,** Neue Beiträge zur Kenntniss des Baues und der Lebensgeschichte der Nematoden. Abhandl. Sächs. Ges. Wissensch. 22, 1887 (p. 567.)

29. **Loman, J. C. C.,** Ueber den Bau von *Bipalium* Stimpson, nebst Beschreibung neuer Arten aus dem Indischen Archipel. Bijdr. tot de Dierkunde, 14, Afl. 1888.

30. **Marion, A. F.,** Recherches sur les Animaux Inferieurs du Golfe de Marseille. Ann. d. Sci. Nat. 1873–74.

31. **Mayer, Paul,** Carcinologische Mittheilungen, VI. Uber den Hermaphroditismus bei einigen Isopoden. Mittheil Zool. Stat. Neapel. I, 1879.

32. **Montgomery, T. H., Jr.,** Stichostemma eilhardi nov. gen. nov. spec. Ein Beitrag zur Kenntniss der Nemertinen. Dissert. Berlin, 1894. (This paper accompanied by plates has appeared in the Zeitschr. f. wiss. Zool. 1895.)

32a. **Moore; Percy, J.,** Hermaphroditism of Prorhynchus. A preliminary Note. Zool. Anz. 1895.

33. **Muller, J.,** Ueber Synapta digitata und die Erzengung von Schnecken in Holothurien.

34. **Nansen, J.,** A Protandric Hermaphrodite (Myxine glutinosa L.). Bergens Museums Aasberetning, 1877–'78.

35. **Peck, J. T.,** On the Anatomy and Histology of Cymbuliopsis calceole. Studies from Biol. Lab. Johns Hopkins Univ. IV (p. 335.)

36. **Pelseneer, P.,** Recherches sur divers Opisthobranches. Mém. Cour. Acad. Belg. 53.

37. **Pelseneer, P.,** Hermaphroditism in Mollusca. Quart. Journ. Micr. Sci. 37, 1894.

38. **Roboz, Z. v.,** Beiträge zur Kenntnis der Cestoden. Zeitschr. f. wiss. Zool. 37, 1882 (p. 263.)

39. **Rywosch, D.,** Ueber die Geschlechtsverhältnisse und den Ban der Geschlechtsorgane der Microstomiden. Zool. Anz. 10, 1887 (p. 66.)

40. **Rywosch, D.,** Die Geschlechtsverhältnisse des Microstoma lineare. Sitz. Ber. Nat. Ges. Dorpat. 8, 1889.

41. **Simroth, H.,** Ueber die Genitalentwicklung der Pulmonaten und die Fortpflanzung des Agriolimax lævis. Zeitschr. f. wiss. Zool. 45, 1887.

42. **Smidt, Ferd.,** Eine neue Species des Genus Graffilla (v. Ihering). Sitz. Ber. Nat. Ges. Dorpat. 8, 1887.

43. **Strassen, O. zur,** Ueber *Filaria rigida,* Vorlaüf. Mittheil. Zool. Anz. 14, 1891 (p. 437.)

44. **Topsent,** (1887.)

45. **Van Beneden, P. J.,** Sur les organes sexuels des Huitres (O. edulis). Compt. rend. Acad. Sci. Paris, XL.

46. **Wheeler, W. M.,** Protandric Hermaphroditism in Myzostoma. Zool. Anz. XVII, 1894.

47. **Wiren, A.,** Studien über die *Solenogastren,* II. Kongl. Svenska Vetensk. Akad. Handl. 25, 1892.

48. **Zschokke, F.,** Studien über den anatomischen und histologischen Bau der Cestoden. Centralbl. f. Bakter. und Parasitk. 1, 1887 (p. 337, 409.)

SPONGES: RECENT AND FOSSIL.

By Joseph F. James, M. D., M. Sc., U. S. Dept. Agriculture, Washington, D. C.

A sponge, while one of the lowest forms in the scale of animal existence, belongs to a class ranging back in time almost to the beginning of organized life. As known in a living state it is an aggregation of individuals, each one minute, but together forming a body often of considerable size. Without power of locomotion; without any differentiation of parts such as obtain in animals of a higher grade, it yet manages to subsist in a great number of places and in the greatest variety of forms. Geology tells us the family has persisted upon the earth since the earliest time of which there is any record; and at no period has it been absent from places suited for the growth of its various members. A few words about living sponges may make plainer a short account of some of the fossil forms.